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Root Grafting and Non-competitive Relationships Between Trees

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The principal relationship between plants is thought to be one of competition for required components of the environment. Thus individuals growing close together are thought to alter each other's environment by utilizing available supplies of water, nutrients, and light; stresses induced by overutilization result in a general reduction of growth and often in the death of some of the competing organisms. This theory is admirably supported by facts gathered not only through centuries of empirical experience in growing plants, but also through more recent experiments designed specifically to test the effects of competition.

Although the competition theory was probably developed through experience gained with herbaceous agricultural plants, it has been widely accepted by forest botanists and used to explain relationships between forest trees. Thus, under certain conditions, the success of some trees and the failure of others is generally ascribed to differences in the competitive ability of the individuals. This idea is the touchstone from which most botanists proceed in their analysis of forest tree behavior. It also underlies the universally accepted idea in forestry that under given environmental conditions each tree has, in theory, an ideal growing space. The regular spacing of trees in a forest tree plantation or in artificially thinned forests is a reflection of this theory.

It now appears that the interpretation of the tree as a strictly individual entity is, in many instances, open to serious question. Evidence amassed, particularly in the last decade, indicates that root grafts or fusions between roots of two or more trees are common. The existence of continuity of conducting tissues between trees opens the possibility that biological activities in one may be directly influenced by another through biophysical and biochemical forces exerted through natural root grafts. These forces exerted directly by one tree on another may play an important role, along with competition, in shaping the nature of the forest community.

Three categories of root grafts occur in nature. Although the most common type involves self grafts or grafts between roots of an individual tree, these are germane to the present discussion only when they enter into complexes of grafts between trees. Interspecific grafts between roots of trees of different species, although of considerable biological interest, are relatively rare so far as is now known. Intraspecific grafts between roots of trees of the same species are common and it is with these that most of the following paragraphs will deal.

For a long time, natural root grafts have been known as a botanical curiosity and reports of their occurrence have appeared sporadically throughout the literature of botany and forestry. These came primarily from direct sightings of grafts or from observations that certain seemingly dead stumps continued to live and grow in diameter. It was discovered that these living stumps were invariably connected to living trees through root grafts—a conclusion confirmed by injection of radioisotopes into stumps and their later detection in adjacent trees (Fig. 14–1). Additional reports are found in the literature of plant pathology where root grafts were found to be responsible for the transmission of disease organisms from tree to tree.

Prior to 1950, although dozens of articles contained reports of root grafts, there was little recognition of their widespread occurrence or their potential significance in forest ecology. Since that time, by means of tracer techniques and excavation, the occurrence and function of root grafts have received increasing study from botanists around the world, particularly in the United States, Finland, and the Soviet Union.

For the past 4 years, the writer has studied root grafting in white pine forests growing on a wide range of sites in New Hampshire, Maine, and Vermont, and the results of this continuing study indicate that grafting is a much more common phenomenon than previously suspected.

In 1957, 84 experimental plots were established in five white pine stands selected to represent different age classes and various soil conditions (Bormann and Graham, 1959). Each plot was composed of a central donor tree, whose top was removed and whose stump was injected with either a radioisotope or dye, and the adjacent potential receptor trees. These were examined periodically for the presence of the injected substance. Of the 81 trees and 3 living stumps injected, 41 were found to be grafted to a total of 54 receptor trees (Table 14–1). These data indicated that root grafting involving 30 to 67 per cent of the injected trees occurred on all sites—regardless of age of stand, soil, or drainage conditions.

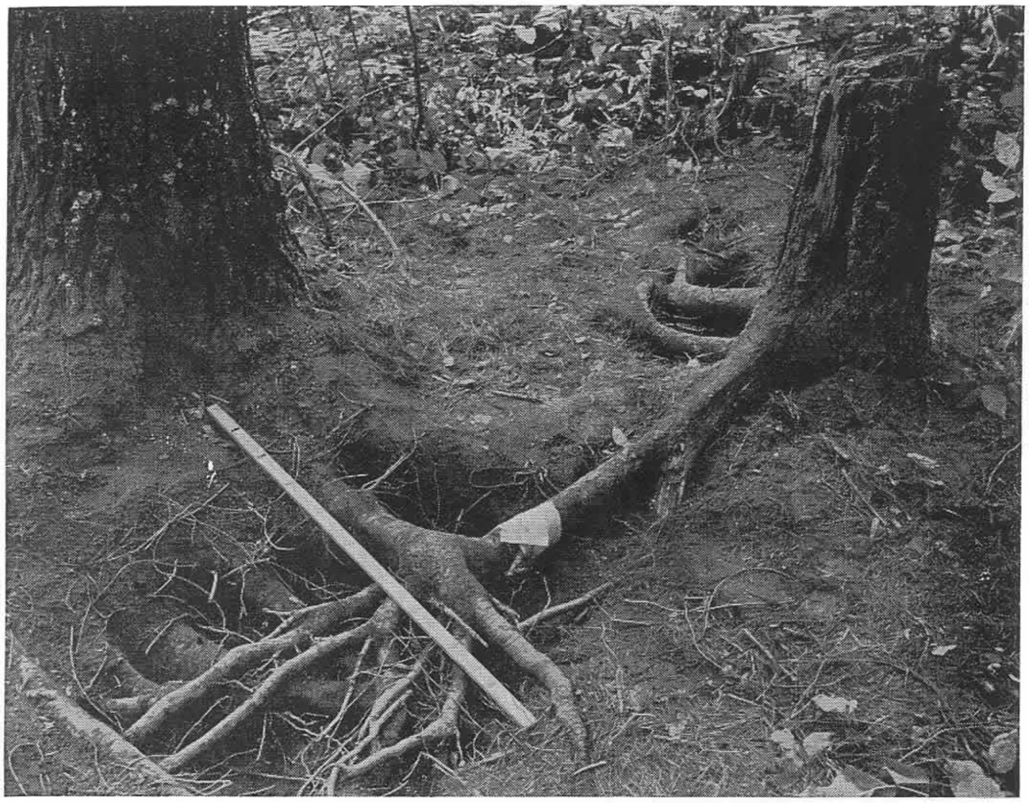

FIG. 14–1. A living stump showing graft connections with the living tree on the left.

Exposure of the root systems on several plots revealed networks of grafts between trees and indicated that often several trees were united rather than two or three, as shown by our detection methods. A union of several trees whose grafted roots were exposed on the surface of a bog is probably characteristic of similar unions found in upland situations—especially in old natural stands (Fig. 14–2). In the bog union, the roots of six large trees are fused into one anastomosing root network.

These results of the injection study were substantiated by other studies on the prevalence of living stumps in natural stands and on

TABLE 14–1

Natural Root Grafts in White Pine Stands, Detected Through Use of Radioisotopes and Dyes. All Stands Located in Northern New England. (From Bormann and Graham, 1959.)

Stand Number	Average Age of Stand (Years)	Density (Stems per 100 m²)	Average d.b.h.(cm.)	Number of Donor Stumps	Number of Donor Stumps Grafted	Number of Receptor Trees
1	15	117	7	20	10	11
2	19	69	8	20	6	7
3	27	30	16	20	10	14
4	39	16	20	9	4	5
5	55	4	31	12	8	14
5	Stumps	4	31	3	3	3
			Total	84	41	54

the per cent of damage incurred by translocation of poison from treated to non-treated trees in white pine stands thinned with silvicides (Fig. 14–3) (Bormann and Graham, 1959). A more recent report indicates that entire quarter acre blocks of 35-year-old, naturally occurring stands were wiped out following thinning with ammate (S. W. Pulitzer, personal communication). Further evidence on the intensity of grafting comes from Professor K. A. Armson who found the roots of all the trees in a 90-year-old white pine stand on thin sandy soil to be fused into a single network (personal communication).

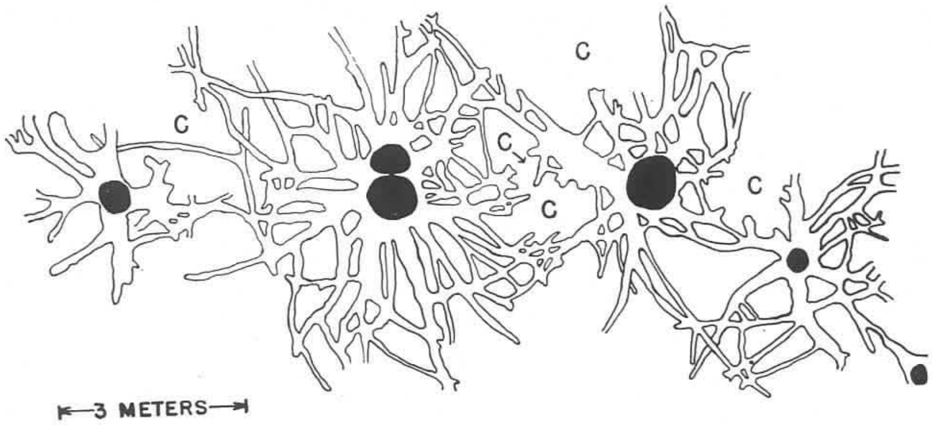

Fig. 14–2. Diagram of a root network exposed on the surface of a deep, partially drained peat soil. Black circles represent stumps and C's indicate areas where some roots have been removed by chopping. Both self-grafts and intraspecific grafts are found in the complex. From Bormann and Graham (1959).

The evidence to date indicates that grafting occurs in stands of all ages, and in stands growing in coarse sand, loams, stony soils, soils free of stones, well-drained soils, poorly drained soils, and extremely wet peat soils. It is concluded that given proper spacing conditions, grafting will occur among white pine trees growing under the whole range of conditions tolerated by the species population.

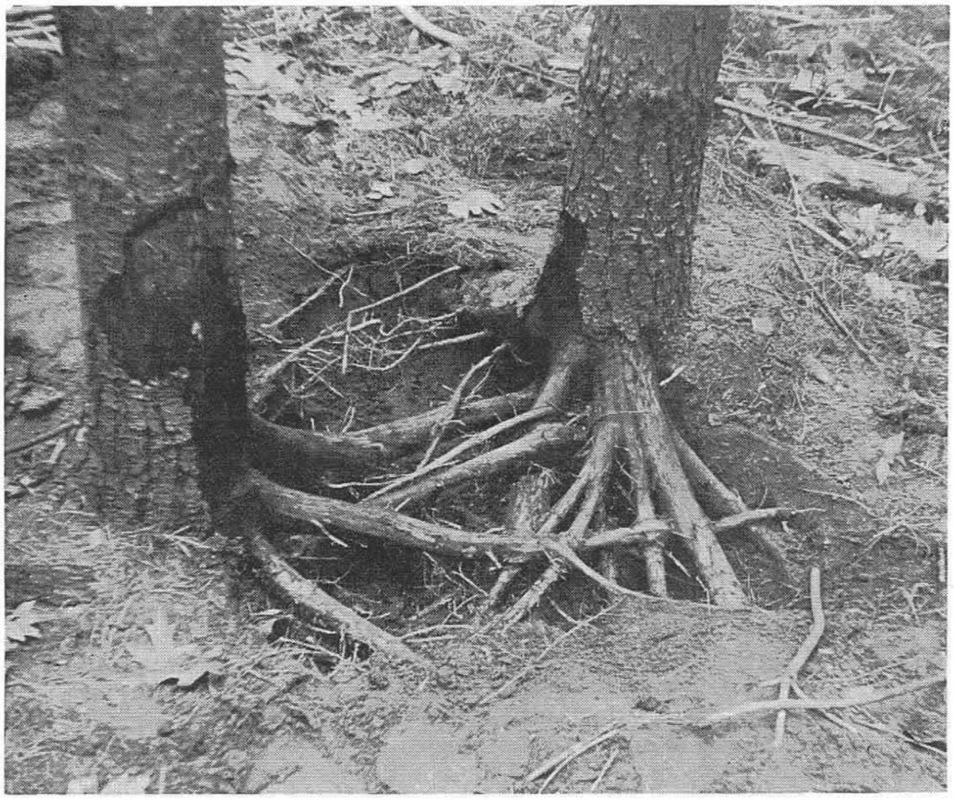

FIG. 14–3. The tree on the right was killed by ammate translocated through natural root grafts from the tree on the left. From Bormann and Graham (1959).

Evidence from other investigations suggests that our results may be applicable to a wide range of forest tree species. Notable work by Yli-Vakkuri (1953) in Finland indicates that up to 28 per cent of the trees in older Scots pine forests are grafted. In the U.S.S.R., Junovidov (1952) has estimated 26, 30, and 45 per cent, respectively, of the trees in young forests of Siberian pine, larch, and fir are grafted. Among 35-year-old trees in a plantation of Crimean pine, Beskaravainya (1956) found 50 per cent of the trees to be grafted. Studying a German spruce stand, Wichmann (1925) found 462 living stumps and 3,334 living trees. Since the root system of each stump was grafted to at least one living tree, and many of the trees were undoubtedly grafted to each other, this stand must have been a maze of root grafts. The extreme of root grafting has been reported by Kuntz and Riker (1956) for dense stands of northern pin oak growing in Wisconsin. Using radioisotope tracers they found practically all trees to be united with their neighbors.

In summation, Graham and Bormann (unpublished) have compiled a bibliography of 171 references containing reports of intraspecific root grafting in 105 species of forest trees. Based on the degree of grafting mentioned in each report and the number of times grafting has been reported for each species, they have concluded that grafting is a common phenomenon in 63 of these species including such important trees as white, red, and Scots pine, European and American beech, Douglas-fir, eastern hemlock, red oak, and American elm. Thus, there seems little doubt that intraspecific root grafting is a widespread phenomenon of considerable potential importance.

The role of intraspecific grafts in the physiology and ecology of grafted trees is slowly unfolding. The movement of water, minerals, food, dyes, and poisons, up to distances of 43 feet between trees, indicates that grafts function in the transport of substances (Bormann, 1959). In a study of the rate of water intake by freshly cut stumps, Graham (1960) found a correlation between the rate of intake and weather conditions conducive to high water losses through the leaves of trees grafted to the stumps. Apparently stresses on the water-conducting system, developed as a result of water loss from the intact trees, were felt throughout the grafted root system and were, in part, responsible for regulating the rate of intake by the stumps.

Another indication of how one tree may influence another is provided by the observation that radioisotopes moving in the root system of one tree are frequently shunted through grafts to the root system of another tree (Yli-Vakkuri 1953, Bormann and Graham, unpublished data). The observation that radioisotopes move predominantly from tall, vigorous oaks to small oaks, has prompted the suggestion that the former may aid in the survival of the latter (Kuntz and Riker, 1956).

To better understand the development of unions of grafted trees within a stand, Bormann and Graham (1959) studied grafting in white pine stands of various ages. Based on these data the following hypothesis is proposed:

Early in the life of a stand, some trees become grafted together in unions, while other trees remain as individuals. As the stand matures and the trees become larger, root systems increase in size, and a union may coalesce with an adjacent union or individual. Throughout this period, the tendency to add new members to the union is counteracted by the death of some of the members. However, death of a tree proceeds from the top down and often the root system remains alive and functional within the graft complex for years after the top has decayed and toppled over. In the older stands, the union is often represented by one to several robust trees surrounded by one to several living stumps (Fig. 14–4). As a particular union matures the more vigorous trees come to dominate the group, while less vigorous companions succumb, leaving only their roots to function in the union. The exact function of a "captured" root system is not known, but it seems likely that it is at first utilized by the dominant tree in the absorption of water and minerals. Later, living stumps may prolong their survival at the expense of the dominant tree and in a sense parasitize it. This is one of the fundamental areas for future research.

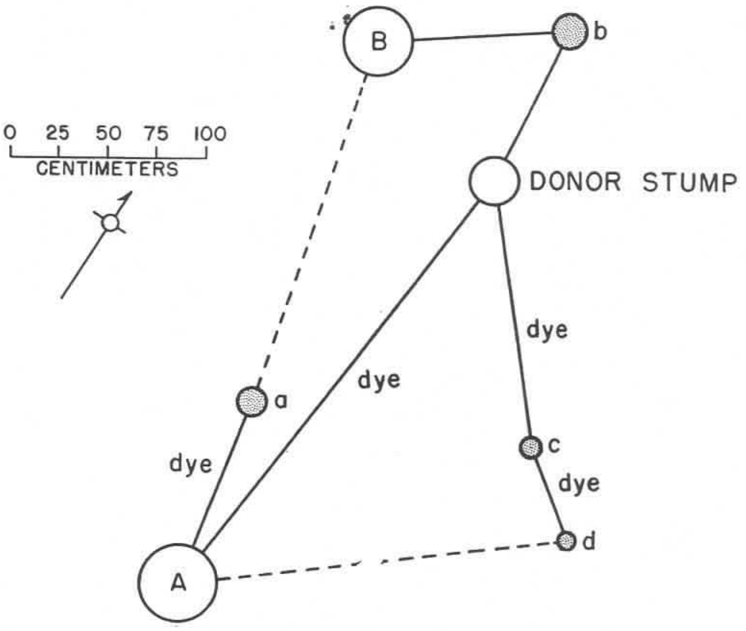

FIG. 14–4. Diagram of a union of trees detected in a 55-year-old stand by means of dye injection. Living trees are represented as open circles, while living stumps are shown as shaded circles. Solid lines mark grafts disclosed by dye transfer and/or excavation. From Bormann and Graham (1959).

The discovery of the mechanisms by which a few trees are able to dominate a union is a major objective. Perhaps because of some initial advantage of size, vigor, or heredity these trees are able to establish gradients that cause water and minerals absorbed by the root complex to move primarily to them at the expense of their less vigorous companions. Another mechanism by which dominant trees may influence smaller trees grafted to them was suggested by the results of recent field work (Bormann, unpublished data).

The initiation, in the spring, of cambial growth within the twigs, branches, and trunk of a tree is thought to be triggered by an auxin moving down the stem from the site of its production in the expanding buds (Wareing, 1951). A study of the stumps of trees detopped in early March and known to be free of grafts with intact trees indicated that, although many stay alive for the first growing season after cutting, none exhibit diameter growth. The cambial zone was always found adjacent to last summer's wood. Microscopic examination of the cambial regions of these stumps indicated that the cells were alive and healthy. Stored food (starch grains) was present in some as was cyclosis. In general, these sections conformed to Abbe and Crafts' (1939) description of the cambial region prior to cambial activation. The failure of the cambium to resume activity was apparently due to the lack of the triggering factor. Conversely, stumps grafted to living trees resumed normal cambial activity probably following the transfer of the triggering factor through grafts from the intact tree. Apparently one tree has been able to initiate activities in the stump of the other. This raises the speculation that large trees whose buds break first would be able to initiate cambial activities in smaller trees grafted to them before their own buds break. The implications of this are not wholly clear, but premature initiation may introduce a serious element of disharmony into the normal processes of development and mobilization of stored foods. Perhaps this is one of the ways that larger trees gradually bring about the demise of the tops of smaller trees while their roots are retained as part of the root complex.

What is the ecological importance of root grafting? Often abandoned or disturbed land is occupied by dense stands composed of a single species; for example, white pine and red spruce in New England; red, white, and jack pine in the Lake States; and loblolly, shortleaf, and longleaf pine in the Southeast. These stands of single species, and others like them throughout the world, are supposed to exhibit competition par excellence since the trees are crowded and each tree has almost identical requirements. Attrition over a period of a few years is great, and often up to 98 per cent of the trees may be eliminated in five to ten decades. The usual explanation for this ecological paring process is severe competition.

Experience with white pine, however, indicates that the importance of competition as a factor in stand development may be severely overrated. It seems likely that competition plays the important role during the first five or ten years of the existence of a stand. Thereafter, unions begin to form and the stand must be visualized as being composed of unions of grafted trees interspersed with non-grafted individuals. The number of trees in any stand occurring in unions or as individuals is primarily a function of the age of the stand and the space between trees. In the extreme, it is conceivable that an entire stand may be united in a single anastomosing root network. Competition may eliminate the less-fit individuals or unions, but, within the unions, which often contain the majority of trees in the stand, forces operating through root grafts will determine which trees will remain as dominant entities.

Whether or not these results apply to other species is a matter for future research, but it seems likely that some of the numerous species where root grafting is common will react in a similar way. In other species, it is probable that root grafting may have different effects; for example, in oak stands root grafts may aid in the survival of smaller trees while in white pine they may hasten the demise of smaller trees.

At any rate, these findings, that many forest trees do not always occur as individual entities, and that biological forces other than competition may play a major role in shaping a developing stand, open a wholly new aspect of basic research in interplant relationships. They also bring into question practices in applied forestry based either on the concept of the forest tree as an individual or on the concept of competition as the dominant biotic force in stand development.

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